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Symposium review: Decomposing efficiency of milk production and maximizing profit*

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ABSTRACT

The dairy industry has focused on maximizing milk yield, as it is believed that this maximizes profit mainly through dilution of maintenance costs. Efficiency of milk production has received, until recently, considerably less attention. The most common method to determine biological efficiency of milk production is feed efficiency (FE), which is defined as the amount of milk produced relative to the amount of nutrients consumed. Economic efficiency is best measured as income over feed cost or gross margin obtained from feed investments. Feed efficiency is affected by a myriad of factors, but overall they could be clustered as follows: (1) physiological status of the cow (e.g., age, state of lactation, health, level of production, environmental conditions), (2) digestive function (e.g., feeding behavior, passage rate, rumen fermentation, rumen and hindgut microbiome), (3) metabolic partitioning (e.g., homeorhesis, insulin sensitivity, hormonal profile), (4) genetics (ultimately dictating the 2 previous aspects), and (5) nutrition (e.g., ration formulation, nutrient balance). Over the years, energy requirements for maintenance seem to have progressively increased, but efficiency of overall nutrient use for milk production has also increased due to dilution of nutrient requirements for maintenance. However, empirical evidence from the literature suggests that marginal increases in milk require progressively greater marginal increases in nutrient supply. Thus, the dilution of maintenance requirements associated with increases in production is partially overcome by a progressive diminishing marginal biological response to incremental energy and protein supplies. Because FE follows the law of diminishing returns, and because marginal feed costs increase progressively with milk production, profits associated with improving milk yield might, in some cases, be considerably lower than expected.
Key words: economics, feed efficiency, income over feed cost, residual feed intake

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INTRODUCTION

The dairy industry has achieved impressive improvements in milk production per cow through continuous advancements in genetics, nutrition, health, and management. In the last decade, world milk production has increased by more than 20%, from 694 million tonnes in 2008 (FAO, 2010) to 843 million tonnes in 2018 (FAO, 2019). However, when this figure is expressed per human on earth, milk production in 2010 was approximately 100 kg/person, and in 2019 was approximately 110 kg/person, just a 10% growth. The strategies to overcome the gap between production and demand for dairy products worldwide are different depending on the geographical region. In less-industrialized regions, the emphasis will likely be placed on improving production (and this by itself will improve efficiency, through dilution of maintenance needs), whereas in areas with highly intensified production systems, the emphasis will likely be progressively placed more on reduction of environmental impact and improvement of profitability through the amelioration of efficiency of milk production (**EMP**) than on increasing milk yield. Nevertheless, even in industrialized regions, an interest may remain in increasing milk production per cow as a means to improve EMP through dilution of nutritional needs for maintenance. However, as we will discuss, doubts exist as to whether this dilution of maintenance evolves linearly or curvilinearly or even whether it may reach a plateau with further increases in milk yield. Efficiency of milk production, defined as the proportion of resources used to sustain production (during the entire production process, including dry cows and heifer rearing) that are actually diverted toward milk, can be measured in terms of natural resources (i.e, feed and water) or economic value, but the underlying biological constraints that influence EMP are similar. From a holistic perspective, EMP is influenced by the quantity and quality of heifers, the quantity and quality of dry cows, the length of the dry period, the length of the rearing period, the quality and adequacy of the feeds provided, the environmental conditions, the longevity of the cows, the amount of feed that is wasted or spoiled, and still other factors. Improving EMP has 2 major consequences: (1) affecting dairy herd profitability, and (2) ameliorating the environmental impact of milk production. Improvements in profits would stem mainly from a wider gap between cost and income, and minimization of environmental impact would be obtained by diverting a greater proportion of nutrients to milk yield (diluting maintenance requirements); for example, the amount of feed used by the US dairy industry (and that of other countries also) to produce 1 L of milk today is 80% less than it was 75 years ago (Capper and Bauman, 2013).

Feed efficiency (**FE**), which reflects the proportion of nutrients consumed by the cow that end up forming part of the milk produced by the animal, is one of the most relevant metrics of EMP. Feed efficiency can be calculated in many ways. The most common, and crude, calculation is milk yield over feed consumed. Alternative forms include energy-corrected milk over feed or energy consumed, or milk protein yield over protein consumed. Residual feed intake (**RFI**), the difference between observed and predicted DMI, has been used, in some instances, as a proxy for FE, where animals with a high RFI would be considered to have a low efficiency (i.e., they eat more than would be expected for a given level of milk production). The prediction models used to estimate RFI vary in the type and number of variables included, but a potential problem with RFI is that it is difficult to ensure that residuals are actually a consequence of deviations in FE rather than just inaccuracies of the mathematical model fitted. Nevertheless, RFI is mainly used in genetic selection schemes, and it would not be advisable to use it the sole metric of FE. At best, RFI could be considered as a partial estimate for FE that is, in theory, independent of parity, body frame, and level of production. For example, in beef cattle, where the concept of RFI has been more extensively used than in dairy cattle, it has been reported that selecting for RFI may not result in improvements in FE but in changes to body composition or appetite (Lines et al., 2014).

In terms of economic relevance, the most important input for milk production is feed, and thus improvements in the proportion of money invested in this asset that is converted into income from milk has a direct and drastic consequence on the profitability of dairy herds. From an economics perspective, FE can be expressed as the ratio between income from milk and investment on feed, or alternatively, as what is commonly referred to as income over feed costs (**IOFC**), which is the difference between milk revenue and feed cost.

Although EMP is affected by a wide variety of factors, both EMP and gross economic returns at the cow level could be decomposed in 5 main aspects: (1) physiological status of the cow (mainly affected by reproduction, health, and environmental conditions), (2) digestive function, (3) metabolic partitioning, (4) genetics (ultimately dictating the 2 previous aspects), and (5) nutrition.

PHYSIOLOGICAL STATUS

Most current dairy production systems worldwide focus on maximizing milk yield and increasing herd size. The trend of increasing farm size has led, in many instances, to herds with a much larger number of heifers than they would actually need to maintain herd size, even in those herds that are no longer growing in size. An excessive number of young stock is costly, both economically and environmentally. Herds typically have more heifers than needed because of (1) a less-than-optimal age at first calving, (2) a relatively high noncompletion rate (proportion of animals that do not reach first calving), and (3) a relatively low retention time in the lactating herd. When age at first calving is delayed, the number of heifers needed in a herd increases, and consequently costs increase due to (1) increased number of feeding days and number of animals fed and (2) decreased FE as age increases (Bach and Ahedo, 2008). Nowadays, with the introduction of genomic selection and sexed semen, producers are progressively changing breeding policies and reducing the number of heifers they rear and using more beef semen in cows with low genetic merit. However, most herds could further reduce young stock numbers by improving the life spans of heifers during lactation. Several studies report failure rates of heifers during the first lactation greater than 15% (Bach, 2011; Cooke et al., 2013; Sherwin et al., 2016). It is unlikely that any other industry could survive with a failure rate of more than 15% of their new products during the first year of reaching the market. Improving the success rate of heifers, in terms of the proportion of animals that reach a second lactation, would, per se, drastically improve the overall EMP of the herd, because the proportion of first-lactation cows in the herd will be reduced, and these cows are less efficient producing milk than are adult cows, as they divert a fraction of the consumed nutrients for development.

The stage of lactation of the cow also influences EMP or IOFC. In early lactation, cows use part of their reserves to sustain milk yield, whereas toward the end, part of the nutrients consumed are diverted toward body reserves, lowering FE. However, the classification of a cow as having a low or high FE relative to the cohorts can change depending on the stage of lactation. For example, important differences in RFI between early- and late-lactation cows have been reported and even described to be negatively correlated (Li et al., 2017).

Additionally, the health status and activity of the immune function of the animal will exert an effect on FE. Increased inflammation status of an animal may partition nutrients away from production (Loor et al., 2005; Bertoni et al., 2008). For instance, low inflammation status of the rumen wall in steers (Reynolds et al., 2017) or of the intestinal wall in broilers (Liu et al., 2019) has been associated with improved growth and FE; and in dairy cows, the energy cost of activating the immune system (by administering lipopolysaccharide) has been reported to be 0.64 g of glucose/kg of metabolic BW per hour (Kvidera et al., 2017).

Lastly, environmental conditions will influence economic returns from cows. When animals are exposed to excessive heat or cold, they divert a considerable amount of energy to maintain body temperature, and consequently less energy is available for milk production. Under elevated environmental temperatures, DMI and milk yield will decrease, but FE is further depressed in heat-stressed cows than in cows kept in thermoneutral temperatures consuming the same amount of feed (Rhoads et al., 2009; Wheelock et al., 2010). Extreme cold weather conditions also affect FE, although considerably less research has been performed on this topic, and the few studies available (Schnier et al., 2003; Angrecka and Herbut, 2016) report decreases in milk of about 1 to 2 kg/d but do not report feed intake and FE.

DIGESTIVE FUNCTION

Feed efficiency has been associated in dairy heifers (Rius et al., 2012), beef steers (Nkrumah et al., 2006), and lactating cows (Potts et al., 2017) with improved digestibility. Feed digestibility is a reflection of both inherent digestibility of the ingredients that compose a ration and the digestive ability of the animal. Feeding highly digestible ingredients should result in improved FE, as a greater proportion of nutrients consumed become available to the animal, but FE also depends on the animal. However, as milk yield increases, DMI also increases, and consequently the passage rate of digesta accelerates, diminishing the proportion of nutrients that the cow can extract from the feed, especially with rations containing large proportions of ingredients with low digestibility, such as mature forages. Potts et al. (2017) have recently evaluated the contribution of digestibility to FE and estimated that it accounts for between 9 and 31% of the variation in RFI for mid-lactation cows fed low-starch diets (14% starch) but none of the variation when cows were fed high-starch diets (approximately 30% starch).

The way cows consume their ration may also influence FE. It seems that inefficient steers eat at slower rates than do efficient ones (Williams et al., 2011; Green et al., 2013). Similarly, in lactating cows, which can devote about 4.5 h/d to eating (Bach et al., 2006; Beauchemin and Yang, 2005), increased eating rates (grams of feed consumed per minute) have also been positively associated with RFI (Connor et al., 2013) and negatively associated with FE (Ben Meir et al., 2018) at similar levels of milk production, which might suggest that the energy that could be spared by devoting less time to eating and more time to lying down is offset by impairments in digestive efficiency.

Lastly, the composition of the rumen microflora can also exert an effect on FE. The ratio between the abundances of *Firmicutes* and *Bacteroidetes* in the guts of mice and humans has been positively associated with obesity (Ley et al., 2006). In cattle, Delgado et al. (2019) have recently shown that the ratio of *Firmicutes* to *Bacteroidetes* in the rumen of dairy cattle is negatively associated with FE. However, other studies have negatively associated *Prevotella* spp.—which belong to *Bacteroidetes*—with FE in dairy cows (Jewell et al., 2015; Bach et al., 2019). Others (Beecher et al., 2014) have positively associated the relative abundance of *Ruminococcus flavefaciens*—which also belongs to *Bacteroidetes*—with digestibility and FE. Overall, it seems that the relations between the microbiome and improvements in FE and digestibly are influenced by the type of diet fed to the cows. Hernandez-Sanabria et al. (2012) reported a positive association between FE and the abundance of *Eubacterium* in rumen fluid, but only when steers were fed a 100% concentrate diet and not when they were fed an 80% concentrate diet. However, Carberry et al. (2012) found a stronger relationship between FE and rumen microbiome when feeding a 100% forage diet than when feeding a 30% forage diet.

METABOLIC PARTITIONING

A major driving force for the continuous improvement in FE in the dairy cow throughout the years has resided in the ability to divert large proportions of nutrients consumed toward milk production, which in turn stimulates the cow to consume more feed (Baumgard et al., 2017). Thus, increases in FE have been basically accomplished through dilution of the proportion of nutrients diverted toward maintenance of the animal (VandeHaar and St-Pierre, 2006). In dairy production, the consensus has been that nutrient requirements for maintenance are fixed (NRC 2001), and nutrients supplied above these fixed requirements are then partitioned among different functions (e.g., growth or milk).

A data set was assembled using articles published in the *Journal of Dairy Science* between 2007 and 2019, with the intention of comparing animal responses to different levels of nutrient supply. A total of 169 studies were compiled, but only 51 articles including 187 treatment means complied with the minimum requirements to be included in the final database (Table 1). The selected studies had to provide at least the CP, NDF, EE, ash, and NE_L content of the ration, and DMI, milk yield, milk fat and protein composition, and BW of cows at the beginning and end of the experiments. Then, the amount of net energy partitioned to support maintenance was calculated as a function of metabolic BW following NRC (2001). The amount of net energy directed toward milk production was calculated based on milk fat and protein yield, also following NRC (2001). To account for the amount of net energy retained or mobilized from the body, it was assumed that cows had a BCS of 3.0 (seldom reported in the literature); therefore, a loss of 1 kg of BW was assumed to supply 4.68 Mcal of NE_L, and a gain of 1 kg of BW was assumed to require 5.34 Mcal of NE_L (NRC, 2001). Then a mixed-effects regression, including study as a random effect, was performed between energy consumed above maintenance (accounting for the energy mobilized or deposited by the animal) and the amount of energy secreted in milk. From Figure 1, a discrepancy can be observed between the theoretical dietary supply of net energy above maintenance needs and the amount of net energy realized in the form of maintenance, milk production, and body mass changes. The overall mean bias of the regression line between these 2 variables was −1.46%, which implies that, in general, the amount of energy realized in milk is lower than could be expected based on consumption of net energy above maintenance (and considering changes in body reserves). Differences between observed and calculated values in Figure 1 could be explained by (1) a discrepancy between the DMI from which the NE_L content of the diet was calculated and the actual DMI (i.e., overestimation of energy supply from the ingredients in the ration), (2) potential changes in efficiency of use of energy for milk, (3) potential underestimation of maintenance energy needs, (4) different BCS than the one assumed in the calculations herein, or (5) potential biases in the NRC (2001) model when estimating dietary energy values based on chemical components of the feeds. Because basal metabolic rate of a cow influences the amount of nutrients that remain available for milk production, it affects FE and IOFC. In dairy cattle, energy requirements can vary by 20% among cows producing similar levels of milk under similar conditions (McNamara, 2015). Dairy cows classified as highly efficient produce less heat (Arndt et al., 2015) as a proportion of gross energy intake (mainly due to dilution of maintenance) and have lower skin surface temperatures than less-efficient cows do (DiGiacomo et al., 2014). Erdmann et al. (2019) have recently compared the energy balance of both dry and lactating cows, determined either experimentally using respiration chambers or using nutritional models (GfE, 2009; NRC, 2001; INRA, 2007), and concluded that the 3 nutritional models evaluated underestimated maintenance energy needs by about 20%. Energy requirements for maintenance in mammals are, in general, determined using equations of the form $\alpha BW^{0.75}$, where in dairy cattle $\alpha = 0.08$ (NRC, 2001), although a recent study (Moraes et al., 2015) proposed that energy requirements for maintenance should be calculated using $\alpha = 0.086$ instead. Using data from the 51 studies described above, average energy requirements for maintenance were calculated as net energy consumed (Mcal/d) − net energy mobilized from or stored in body reserves (Mcal/d) − net energy excreted in milk (Mcal/d). The calculation rendered a similar value (0.087 Mcal of NE_L/kg of metabolic BW) to the one reported by Moraes et al. (2015). Increases in mammary metabolic rate necessary to sustain milk synthesis imply changes in extramammary metabolism to ensure sufficient nutrient supply to the mammary gland (Baumgard et al., 2017) and, thus, potentially greater nutrient demands for basal metabolism. In mice, individuals with a high running capacity have a greater basal metabolic rate because they have a greater "metabolic machinery" (i.e., more cells, enzymes, transporters, organelles) to maintain (Rolfe and Brown, 1997). Similarly, in cattle, several authors (Yan et al., 1997; Agnew and Yan, 2000; Moraes et al., 2015) have reported an increase in maintenance needs as milk production has increased throughout the years. Philosophically, the increases in nutrient (both energy and protein) demands associated with extramammary tissues could also be considered production needs, but NRC (2001) and other models do not have equations to account for these nutrient needs beyond differences in body mass (which would then be reflected as

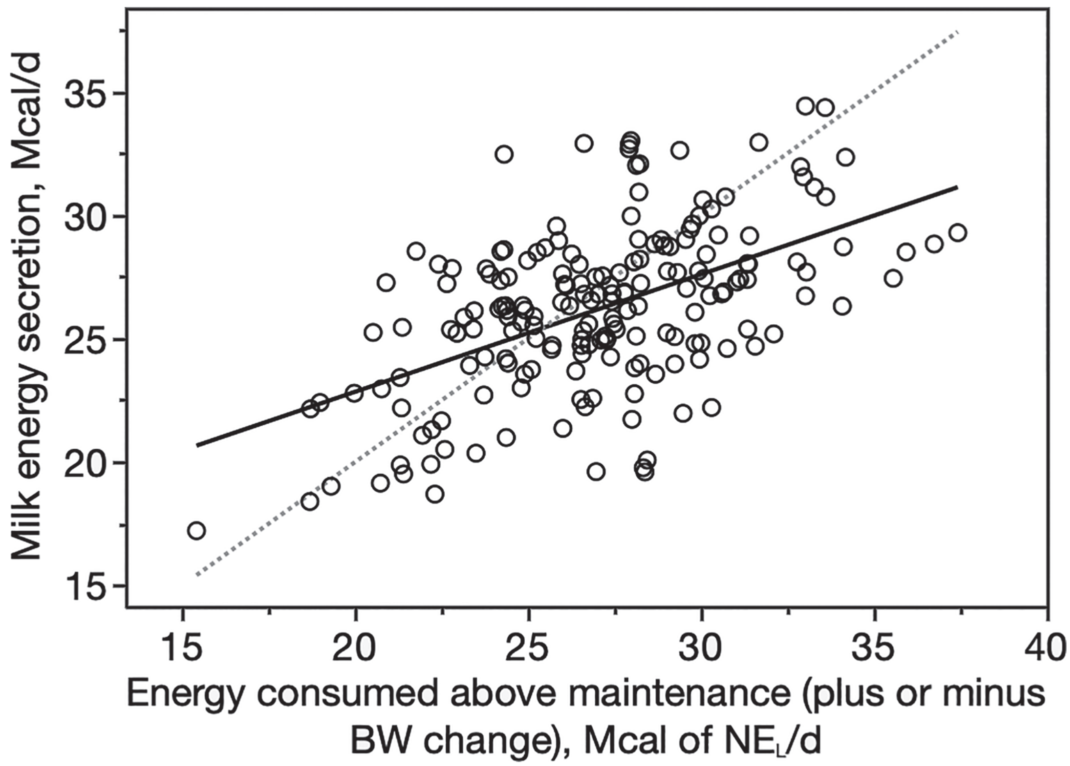

Figure 1. Relationship (solid line) between average net energy consumed above maintenance and derived from or stored as body reserves and average net energy secreted in milk ($R^2 = 0.29$). Dotted line depicts a hypothetical 1:1 relationship. Data from studies 1 to 51, listed in Table 1.

maintenance needs). Recently, however, Sauvant et al. (2015) proposed a variable efficiency of conversion of metabolizable protein to cover increased maintenance needs as production increases. In summary, the concept that maintenance energy and protein requirements are constant for a given metabolic BW could be challenged, which would have implications on FE and economic returns, as discussed later.

Regarding nutrient needs for milk production, the NRC (2001) uses a fixed amount of energy and protein for every liter of fat- and protein-corrected milk produced, with constant efficiencies of conversion from metabolizable protein or energy to net protein or energy. However, evidence form the literature suggest that such efficiency may not be constant. From the data set of 51 studies described above, regressing net energy

Table 1. Studies used to contrast milk energy outputs and net energy consumption in dairy cattle (n = 51)

1. Abdelqader et al. (2009)	18. Dschaak et al. (2011)	35. Naderi et al. (2016)
2. Aguerre et al. (2011)	19. Faciola and Broderick (2014)	36. Nursoy et al. (2018)
3. Aguerre et al. (2016)	20. Fagundes et al. (2018)	37. Potts et al. (2015)
4. Akins and Shaver (2014)	21. Giallongo et al. (2016)	38. Ranathunga et al. (2018)
5. Akins et al. (2014)	22. Harper et al. (2018)	39. Rius et al. (2010)
6. Alstrup et al. (2014)	23. Hart et al. (2014)	40. Romero et al. (2016)
7. Arriola et al. (2011)	24. Kanjanapruthipong et al. (2015)	41. Siverson et al. (2014)
8. Bahrami-Yekdangi et al. (2014)	25. Kargar et al. (2015)	42. Sun et al. (2019)
9. Boerman et al. (2015)	26. Knowlton et al. (2007)	43. Tassoul and Shaver (2009)
10. Borucki Castro et al. (2008)	27. Kung et al. (2008)	44. Testroet et al. (2018)
11. Broderick et al. (2007)	28. Liang et al. (2019)	45. Vander Pol et al. (2008)
12. Bruns et al. (2015)	29. Luan et al. (2015)	46. Van Knegsel et al. (2007)
13. Calsamiglia et al. (2007)	30. Manthey et al. (2016)	47. Wang et al. (2010)
14. Casperson et al. (2018)	31. McCormick et al. (2011)	48. Wang et al. (2018)
15. Chacher et al. (2014)	32. Miller et al. (2009)	49. Weiss (2012)
16. do Prado et al. (2016)	33. Mjoun et al. (2010)	50. Weiss (2019)
17. Donkin et al. (2009)	34. Morris et al. (2018)	51. Zilio et al. (2019)

consumption above maintenance compared with milk energy secretion yielded a quadratic relationship [$R^2 = 0.33$; root mean squared error (**RMSE**) = 2.74 Mcal/d; $P < 0.01$; solid line in Figure 2] of the form

$$\textit{Milk energy secretion, Mcal/d} = 2.682 + 1.084 \times \textit{NE}_L \textit{ above maintenance} - 0.0091 \times \textit{NE}_L \textit{ above maintenance}^2.$$

The quadratic term was significant ($P < 0.05$), but a straight-line model could also be fitted to the data (dashed line in Figure 2), although with a slightly smaller coefficient of determination ($R^2 = 0.31$) and a slightly greater RMSE (2.77 Mcal/d). Part of the curvature of the solid line in Figure 2 could be explained by the type of NE_L reported in the studies. Only studies 2, 3, 4, 8, 10, 11, 13, 14, 19, 28, 36, 37, 42, and 50 from Table 1 indicated that energy was calculated at the level of observed intake; the remaining studies either did not specify or provided a fixed NE_L not corrected for cows' level of intake. When performing the same regression analysis with only the 14 studies reporting discounted energy values (Figure 3), the quadratic term (solid line in Figure 3) became nonsignificant ($P = 0.31$), although the coefficient of determination was slightly greater ($R^2 = 0.26$) and the RMSE slightly lower (1.74 Mcal/d) than those obtained with a straight line (dashed line in Figure 3; $R^2 = 0.24$; RMSE = 1.75 Mcal/d). Therefore, it could be argued that part of the curvature observed in Figure 2 is a consequence of the lack of discounting of NE_L as DMI increases, but as discussed later, there may be additional reasons for that curvature.

Efficiency of protein utilization (the proportion of CP consumed that is recovered in milk protein) in dairy cattle ranges between 18 to 19 (Penner et al., 2009; Rhoads et al., 2009) and 42 to 44% (Nursoy et al., 2018; Nichols et al., 2019). Differences in efficiency of protein utilization also seem to be affected by the level of production. For example, Whitelaw et al. (1986) reported that the infusion of 200 g/d of casein increased milk protein yield by 81 g/d; whereas a 600-g infusion increased milk protein yield by only 158 g/d (instead of 243 g/d, had the marginal response being linear). Early studies (Brody, 1945; Van Es, 1978) and more recent ones (Jensen et al., 2015; Arriola Apelo et al., 2014; Daniel et al., 2016) have incorporated diminishing efficiencies of utilization of both metabolizable protein (Daniel et al., 2017) and energy (Jensen et al., 2015) with increasing milk production. The consequences of this pattern of diminishing returns with increasing supplies of protein are double: on one side it may increase

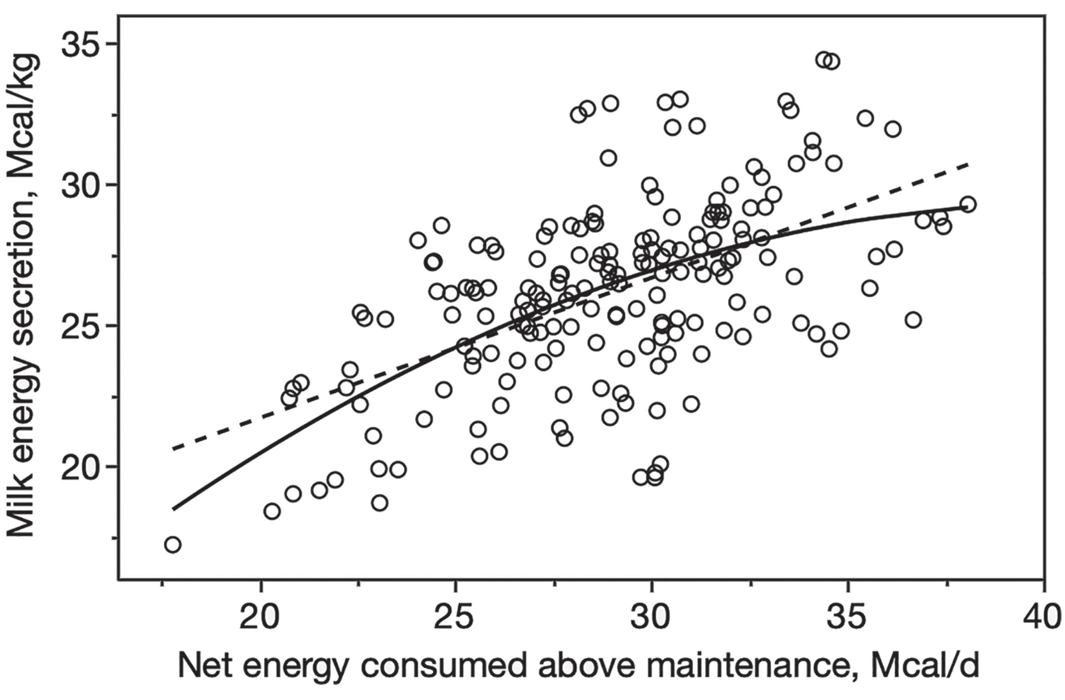

Figure 2. Relationship between net energy consumed above maintenance and energy secreted in milk. Solid line: *Milk energy secretion, Mcal/d* = 2.682 + 1.084 × $\textit{NE}_L$ *above maintenance* − 0.0091 × $\textit{NE}_L$ *above maintenance*^{2}; $R^2 = 0.33$, *P*-value < 0.001. Dashed line: *Milk energy secretion, Mcal/d* = 11.75 + 0.498 × $\textit{NE}_L$ *above maintenance*; $R^2 = 0.31$, *P*-value < 0.001. Data from studies 1 to 51, listed in Table 1.

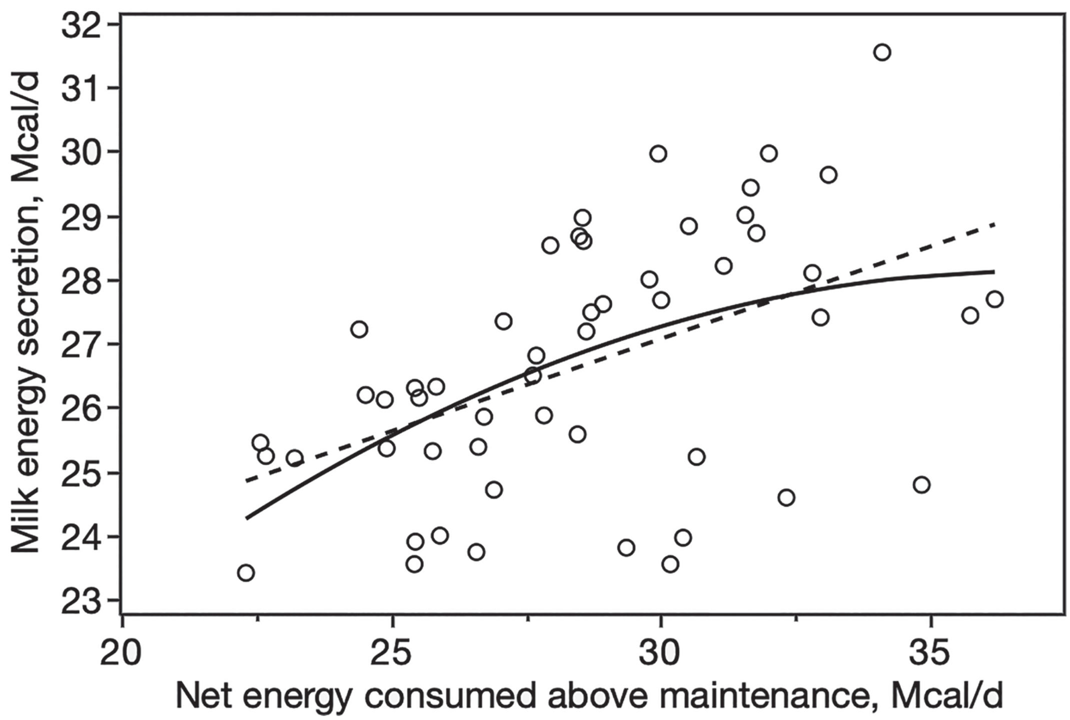

Figure 3. Relationship between net energy consumed above maintenance and energy secreted in milk. Solid line: *Milk energy secretion, Mcal/d* = 3.41 + 1.340 × NE_L *above maintenance* − 0.018 × NE_L *above maintenance*^{2}; R^2 = 0.26, *P*-value < 0.001. Dashed line: *Milk energy secretion, Mcal/d* = 18.41 + 0.289 × NE_L *above maintenance*; R^2 = 0.24, *P*-value < 0.001. Data from studies 2, 3, 4, 8, 10, 11, 13, 14, 19, 28, 36, 37, 42, and 50, listed in Table 1.

N excretion to the environment, and on the other it may reduce marginal IOFC gains.

The decaying overall marginal improvements in efficiencies of using energy or N as supply increases could be due to the fact that marginal increases in energy or N supply are used with marginal diminishing efficiencies to sustain production. Beyond changes in digestibility due to differences in digesta passage rate, this diminishing marginal efficiency improvement could be partly explained by both potential changes in the mammary gland and potential changes in the intermediary metabolism of the animal. For example, Guinard and Rulquin (1995) reported a quadratic decrease in mammary blood flow as the amount of infused Met increased, with a concomitant decrease in extraction rate; thus, extraction rate of Met by the udder remained unchanged. Several studies (Rigout et al., 2003; Lemosquet et al., 2004) have reported that a progressive supply of glucose via duodenal infusion results in a progressive decline in marginal efficiency of glucose utilization to produce lactose in the mammary gland, which leads to a curvilinear (i.e., diminishing returns) increase in milk yield. In terms of nonmammary tissues, the extraction of amino acids by the liver relative to portal absorption increases with amino acid supply, and thus the amount of available amino acids to the cow is frequently smaller than the increase in absorption (Guerino et al., 1991).

GENETICS

Both digestive function and metabolic partitioning are influenced, in part, by genetics. Feed efficiency is currently among the most-sought traits in dairy cattle, due to its relationship with economic returns and stewardship toward the environment through improved use of land and economic resources to produce milk. Just as exercise capacity is a heritable trait (Fagard et al., 1991; Ren et al., 2013), FE, which could be considered a trait for metabolic fitness, should also be heritable. Hurley et al. (2018) have recently shown that phenotypic improvements in feed intake and FE can be achieved through genetic selection. However, it would not be advisable to select solely for FE, because that would result in cows that are in an excessive negative energy balance in early lactation, which could lead to poor reproductive performance (Collard et al., 2000; Bach, 2019) and metabolic upsets (Baumgard et al., 2017). Interestingly, despite the fact that FE has not been directly selected for in dairy cattle, it has doubled in the last 50 years. This improvement has basically been accomplished through increases in milk production brought about by advances in genetics, nutrition, management, and health. However, because the improvements in FE diminish with each marginal increase in milk yield, continued FE amelioration through more milk seems implausible (VandeHaar et al., 2016).

Most genetic studies have focused on classifying cows based on efficiency in mid-lactation cows (around 130 DIM). However, Daniel et al. (2017) reported important changes in FE within cows fed the same ration as lactation stage progressed, and Hurley et al. (2017) found that the greatest heritability for FE (estimated either as residual energy production or as energy conversion efficiency) was obtained after around 250 DIM. Perhaps phenotyping FE toward the end of lactation would be a more sensible strategy to assess the ability of a cow to divert nutrients from milk production over to other metabolic functions or body reserves, which, as discussed later, has important economic implications.

NUTRITION

Because feed costs represent more than 50% of the total cost of producing milk (USDA-NASS, 2015), the efficiency with which feed is used to produce milk has bold economic consequences. Economic returns can be improved by either maximizing milk income for a given fixed economic investment or minimizing economic inputs while maintaining fixed revenues from milk—or even, especially in high-volatility markets, slightly decreasing it. Despite the importance of FE on profitability and environmental impact, total milk yield is considered the most important factor in total farm profitability (Liang and Cabrera, 2015), because as milk yield increases the proportion of total farm fixed expenses decrease. Therefore, even if an optimal production, which would maximize FE is reached, economics may still favor greater production per cow to dilute fixed costs, provided feed costs are reasonable (VandeHaar and St-Pierre, 2006). For this reason, the most relevant aspect to ensure when seeking maximum milk yield is that marginal IOFC is positive, because if marginal gains from marginal milk are neutral or negative, it would be impossible to pay for fixed costs by increasing milk yield.

Under a situation in which dilution of maintenance needs are partially offset by progressively marginal diminishing improvements in milk yield per marginal unit of nutrient consumed and potential concomitant marginal increases in maintenance needs, the economic returns from further increases in production might be lower than expected. Table 2 depicts different IOFC derived using 3 scenarios and assuming a milk price of €0.32/kg. Scenario A: feed costs and efficiency of utilization of nutrients are fixed (a common scenario found in popular press); scenario B: marginal feed costs increase as milk production increases, but marginal efficiency of utilization of nutrients remains constant; and scenario C: a dynamic scenario in which both marginal feed costs and efficiency of utilization of nutrients for milk production increase, but the latter does so at a diminishing rate. In scenario A, according to NRC (2001), a ration for a 640-kg cow producing 29 kg of milk should contain 1.40 Mcal of NE_L/kg, which could cost €0.204/kg, and, because every marginal increase in milk needs 0.71 Mcal of NE_L, 0.51 kg of marginal feed (0.71/1.40) would be needed to support a 1-kg marginal increase in milk yield, which would generate a marginal IOFC of €0.216. This marginal IOFC would always be the same, regardless of basal milk production. In scenario B it is assumed that, to increase milk yield, a richer (or more nutrient-dense) feed needs to be offered. Thus, as yield increases from 29 to 50 kg, the feed offered to cows must progressively increase in nutrient density, and because the amount of feed needed for each additional marginal increase in milk decreases, FE progressively increases. However, because feed costs increase with the level of production, marginal IOFC increases when improving production from 35 to 36 kg of milk but decreases from 49 to 50 kg with respect to marginal IOFC from 28 to 29 kg. Therefore, in this scenario, maximizing FE will not maximize marginal IOFC. Nevertheless, because marginal IOFC is still positive, marginal milk increases above 49 kg will still generate profit. Lastly, scenario C is similar to scenario B, but assuming that marginal increases in milk require marginally greater supplies of nutrients (due to both marginal increases in maintenance needs and marginal diminishing improvement in efficiency of nutrient use), and because the amount of marginal feed needed (and its cost) increases as milk production increases, marginal IOFC declines according to the law of diminishing returns (Table 2). But, again, because marginal IOFC is still positive, marginal milk increases of more than 49 kg will still generate profit, and thus, in theory, such increases remain worthwhile to pursue.

The calculations discussed thus far are for a single cow. Nowadays, most cows are fed total or partial mixed rations. The assumption when feeding a TMR is that, theoretically, each mouthful of feed the cow consumes contains a balanced combination of nutrients. However, when feeding a TMR to a group of cows, nutrient supply progressively becomes imbalanced as milk yield deviates from that used to formulate the TMR (Bach and Cabrera, 2017), which will influence overall FE and IOFC of the group. In this regard, one of the most important steps in ration formulation, quite often neglected, is determining the level of milk yield for which a TMR should be formulated. Deciding the optimum level of nutrients for a group of cows is not trivial. Some dairy consultants consider the deviation around the mean milk yield in a group of cows and then set the target production to cover approximately 80% of the cows in a given group, following the recommendations from Stallings and McGilliard (1984), who proposed to use a lead factor (multiplicative scalar) based on the 83rd percentile method (average production plus 1 SD) as a production target. As an example, following this criterion, a ration for a virtual group of 228 cows with an average BW of 638 kg and an average milk production of 38 kg/d and a standard deviation of 7.0 kg/d should cover 45 kg of milk. Beyond the economic consequences, which will be discussed later, formulating a ration for a given level of production influences the proportion of cows that are overfed and, thus, the overall FE and IOFC of the group. Formulating a TMR for a generous level of production will increase the proportion of cows that will increase their body reserves, leading to a decrease in FE (i.e., less nutrients will be partitioned to milk) but also in the overall EMP of the herd, because a lower proportion of the nutrients initially consumed and stored in cows will then be converted back to milk. Furthermore, overfeeding cows not only impairs FE; it may also compromise milking and reproductive performance in the next lactation, as cows that are overconditioned lose more BW after calving, and this has been associated with poor reproductive performance (Carvalho et al., 2014). Therefore, feeding a TMR that results in a large proportion of cows being overfed is likely to (1) increase the negative environmental impacts of production, (2) reduce economic returns, (3) increase the prevalence of metabolic upsets after calving due to the association between excessive body condition and postpartum metabolic afflictions (Vanholder et al., 2015), and (4) hinder reproductive performance (Carvalho et al., 2014; Bach, 2019).

The consequences of feeding a ration for different production levels to the group of 228 cows described above was evaluated under the following assumptions: first, that the cost of formulating a ration for 35 kg of milk (covering the needs of approx. 30% of the cows) was €0.207/kg, for 45 kg (covering the needs of 83% of the cows) was €0.218/kg, and for 42 kg (meeting the needs of 70% of the cows) was €0.212/kg; milk price was €0.32/kg; and all cows would behave, in terms of DMI and milk yield, according to NRC (2001) with certain biological variation or stochasticity. That is, cows producing $\leq$35, $\leq$42, or $\leq$45 kg/d of milk would continue to produce that milk plus 50 $\pm$ 3% of the excess of consumed energy that would also be diverted to milk (the remaining 50% would go to body reserves), and those that were initially producing >35, >42 or >45 kg/d of milk would then produce the amount of milk allowed by the NE_L density of the ration plus about 30 $\pm$ 3% of the deficit of energy that could be derived from body reserves (i.e., a cow with an energy balance

Table 2. Theoretical marginal income over feed cost (IOFC) obtained from a marginal increase of 1 kg of milk (3.65% fat and 3.20% protein at €0.32/kg) from a 640-kg cow at 3 different levels of production, following NRC (2001) or empirical equations derived from literature observations

Item	Low (28 to 29 kg/d)	Moderate (35 to 36 kg/d)	High (49 to 50 kg/d)
Scenario A: Based on NRC (2001) and fixed feed costs			
Marginal NE_L needs, Mcal	0.71	0.71	0.71
Marginal feed (1.40 Mcal of NE_L/kg) needed, kg	0.51	0.51	0.51
Feed cost, €/kg (ration for 29 kg of milk/d)	0.204	0.204	0.204
Marginal IOFC, €	0.216	0.216	0.216
Scenario B: Based on NRC (2001) and variable feed costs			
Marginal NE_L needs, Mcal	0.71	0.71	0.71
Marginal feed needed,[1] kg	0.51 (1.40)	0.48 (1.47)	0.46 (1.56)
Feed cost, €/kg (ration for each level of production)	0.204	0.207	0.235
Marginal IOFC, €	0.217	0.221	0.212
Scenario C: Based on variable needs and variable feed costs			
Marginal NE_L needs,[2] Mcal	1.00	1.14	1.60
Marginal feed needed,[1] kg	0.72 (1.40)	0.78 (1.47)	1.03 (1.56)
Feed cost, €/kg (ration for each level of production)	0.204	0.207	0.235
Marginal IOFC, €	0.173	0.158	0.078

[1]Marginal feed needed was calculated as follows: marginal energy needs/energy density of the feed. Values in parentheses indicate the NE_L content of the feed (Mcal/kg), which was estimated by formulating a ration for 29, 36, or 50 kg of milk/d, following NRC (2001).

[2]Marginal NE_L needs were calculated as follows: milk energy milk content (e.g., 0.71 Mcal/kg)/(marginal milk energy response/milk energy content). Marginal milk energy response was calculated as $2.682 + 1.084 \times NE_L\ above\ maintenance - 0.0091 \times NE_L\ above\ maintenance^2$, assuming a 640-kg cow producing 28 vs. 29, 35 vs. 36, or 49 vs. 50 kg of milk with 3.65% fat and 3.20% protein, and no change in BW.

of −0.5 Mcal of NE_L, would divert 0.15 Mcal of NE_L from her reserves toward milk, which would support ~0.2 kg of milk). Furthermore, it was assumed that the DMI of all cows would improve by 3% when cows were fed a more nutrient-dense ration and the NE_L content of the diet was adjusted for the DMI of each cow. Under the premises described above, feeding the 228 cows the ration for 35 kg of milk would lead to an average milk yield of 37.4 kg/d and a FE of 1.46 (Figure 4), the ration for 42 kg of milk would result in an average milk yield of 38.6 kg/d and a FE of 1.51 (Figure 4), and the ration for 45 kg would sustain an average milk yield of 39.1 kg/d and a greater FE of 1.53 (Figure 4). Thus, as milk yield increases, FE also increases—although, as discussed above, following the law of marginal diminishing returns. But economic efficiency (i.e., IOFC) did not follow the same pattern. Because the proportion of cows that would be overfed as the dietary milk allowance increases would substantially increase, IOFC for the ration covering 35 kg of milk/d would be €6.77/d; for 42 kg would be €6.96/d; and for 45 kg would be €6.95/d (Figure 4). The decrease in IOFC with a richer ration (i.e., for 45 vs. 42 kg of milk/d) despite the increase of 0.5 kg of marginal milk and 0.2 in FE is due to the fact that slightly more than 70% of the cows fed the 45-kg ration would yield slightly less IOFC than those fed the ration for 42 kg, and the approximately 20% of the cows that generate more IOFC with the 45-kg ration would not offset the loss in gross margin from the lower-producing animals (Figure 5). Thus, when feeding groups of cows, maximizing milk yield or FE may not always result in improved economic efficiency or IOFC. Different outcomes could be obtained if a different partition of the surplus energy consumed between additional milk or body reserves were considered, or if the difference in unitary cost between the 42- and 45-kg ration were smaller, which emphasizes the need to adapt the ration parameters when performing this exercise, to the genetic capacity (e.g., milking response) of the animals, variability in milk production among cows, and different feed costs and milk prices.

Lastly, another relevant factor influencing profits from a herd is whether lactating cows are fed a single TMR or are distributed in several groups and fed different TMR for different levels of production, which has long been shown to benefit IOFC (Smith et al., 1978). A survey in the United States reported that 63% of large dairies fed different rations according to lactation number, stage of lactation, or production level (NAHMS, 2014). However, to maximize profits, McGilliard et al. (1983) proposed not to group cows based on milk production but on energy and protein needs, using clustering algorithms. The most extreme (and unpractical) scenario would be to formulate and feed a specific TMR for each cow in a herd. For example, balancing 228 individual rations for each of the 228 cows described above, following NRC (2001), would render an average IOFC of €7.81/d, assuming a milk price of €0.32/kg. But a more practical strategy would be to group cows in such a way that average IOFC from the entire herd would be as close as possible to the "maximum" €7.81/d. Using this approach, the 228 cows described previously were split into 3 groups (high, medium, and low, based on NE_L and N requirements). With this approach, the 228 were distributed in groups of 60, 88, and 80 animals, respectively, and 3 rations

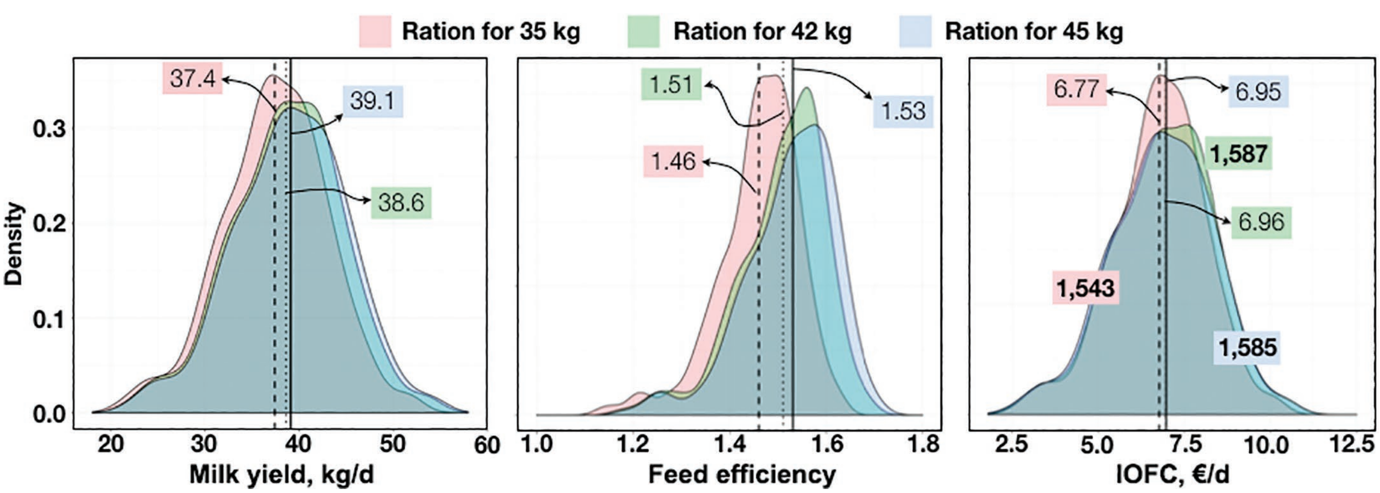

Figure 4. Density plots for expected milk yield, feed efficiency, and income over feed cost (IOFC) of a simulated population of 228 lactating dairy cows with an initial average milk yield of 38 kg/d and SD of 7.0 kg, fed rations formulated to support 35, 42, and 45 kg of milk/d following NRC (2001). Values in boldface denote daily IOFC for all 228 cows. Milk price was assumed to be €0.32/kg, and the expected cost of the ration for 35, 42, and 45 kg of milk was €0.207, 0.212, and 0.218/kg, respectively.

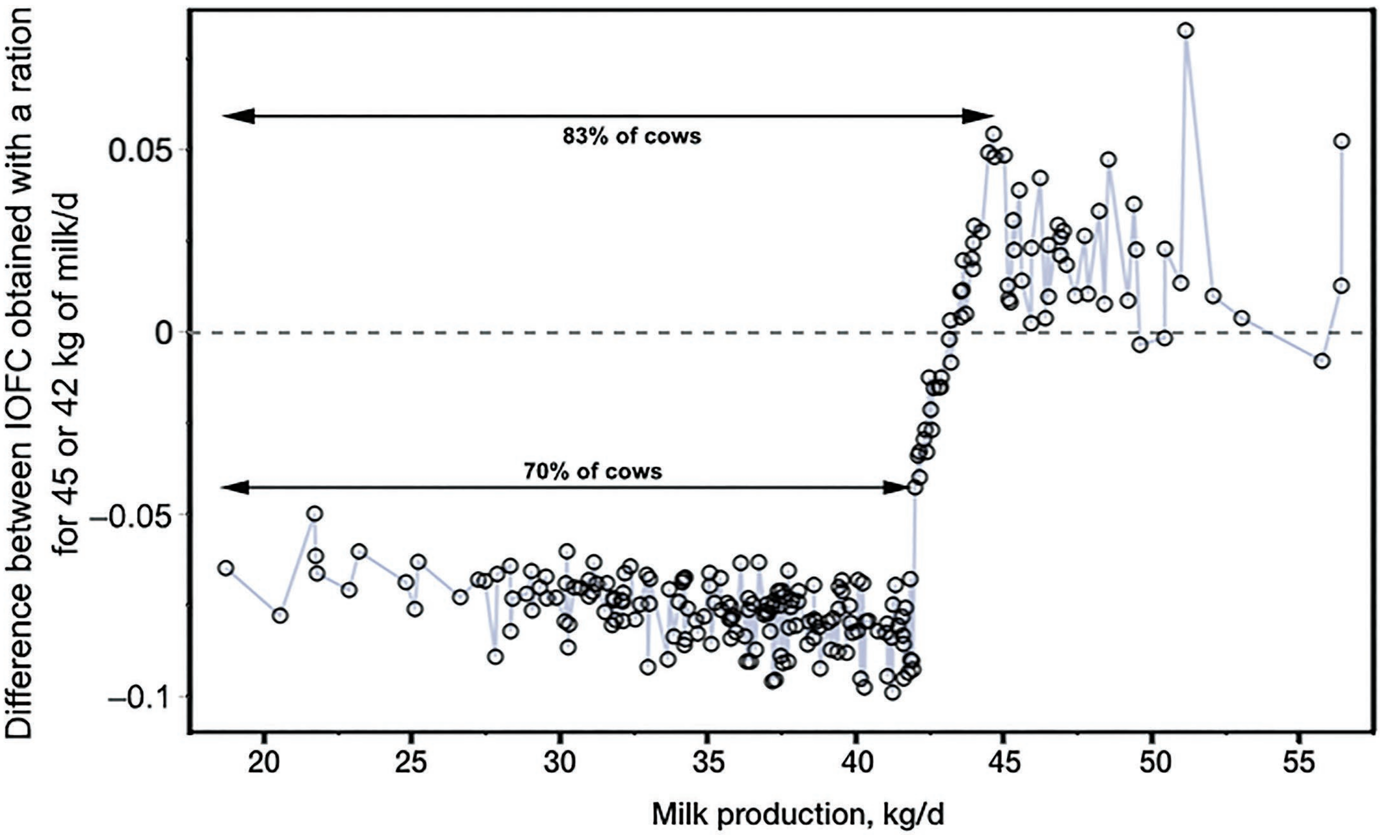

Figure 5. Expected difference in income over feed costs (IOFC) obtained from each dairy cow in a group of 228 animals initially producing an average of 38 kg of milk/d, with SD 7 kg/d, fed a ration formulated for 42 or 45 kg of milk/d. Milk price was assumed to be €0.32/kg; cost of the ration for 42-kg milk yield was €0.212/kg, and that of the ration for 45-kg milk yield was €0.218/kg.

were formulated, following NRC (2001), to cover the needs of 70% of the cows in each group, assuming the same performance responses as above (i.e., following NRC, 2001, and mobilizing or depositing energy reserves depending on energy balance). If the low group was fed a ration for 33.7 kg of milk costing €0.205/kg, it would produce 32.4 kg/d with an IOFC of €5.68/cow. If the medium group was fed a ration for 41.1 kg of milk costing €0.210/kg, it would produce 40.3 kg/d with an IOFC of €7.48/cow. Lastly, if the high group was fed a ration covering 47.6 kg/d of milk and costing €0.228/kg, it would produce 47.1 kg of milk/d with an IOFC of €8.50/cow. The weighted average IOFC of the 3 groups would be €7.13/d, still lower than the theoretical maximum (€7.81/d) but substantially greater than when all cows were fed in a single group (approx. €6.96/d).

LIMITATIONS AND FUTURE RESEARCH

Continuous improvements in genetics as well as management, health, and nutrition have allowed large volumes of milk to be obtained from dairy cows. However, the assumption that more milk will translate into more profit could be challenged under some circumstances. Because cows have not been directly selected for FE, improvements in milk production have been accomplished through increases in feed intake. In this regard, a need remains for more information about the dynamics of feed digestibility and changes in the gut microbiome in cows consuming copious amounts of DM. There has been some debate about the accuracy of the discount of nutrient availability in the NRC (2001) as DMI increases and its implications for economics and for the performance of dairy cattle (VandeHaar and St-Pierre, 2006; Huhtanen et al., 2009), but more work is still needed in this area. Furthermore, as milk yield increases, cows need to partition more nutrients to the mammary gland. Data from the literature seem to indicate that the amount of energy realized in milk is lower than could be expected based on energy consumed. Part of this discrepancy might be due to an underestimation of energy needs for maintenance. Another part could also be due to potential decaying efficiencies of conversion into milk of both energy and protein consumed as a consequence of both a reduction in digestibility (due to increased intake) as well as changes in intermediary and mammary metabolism. In this regard, a need remains to provide better descriptions of the calculations used to assign energy values to feeds reported in the literature. Although evidence exists in the literature that maintenance requirements of dairy cows seem to increase with milk yield (Moraes et al., 2015; Erdmann et al., 2019), and other evidence indicates that protein and energy once absorbed (thus, independent of potential losses in digestion) are used with decaying efficiencies to sustain milk yield (Whitelaw et al., 1986; Jensen et al., 2015), further research is also needed in this area to build equations that can account for metabolic activity beyond body mass—or, alternatively, to modify the equations for calculating nutrient requirements for milk production.

In this article, we have presented several scenarios reflecting different assumptions. First, in scenario C of Table 2, we assumed that marginal increases in milk require marginally greater supplies of nutrients due to both increases in marginal maintenance needs and marginal diminishing improvement in efficiency of nutrient use. The outcome of scenario C would be closer to that of scenario B in Table 2 if these assumptions prove wrong and no decaying efficiency of nutrient utilization occurs with increasing milk yields. The second set of assumptions used herein pertained to animal responses once presented with a given ration. We arbitrarily assumed that cows fed an excess of energy would continue to produce the same amount of milk as before a dietary change, plus 50 ± 3% of the excess of energy consumed that would be diverted to milk (the remaining 50% would be stored as body reserves). Those cows fed a ration that provided an insufficient amount of nutrients would produce the amount of milk allowed by the NE_L density of the ration, plus about 30 ± 3% of the energy deficit that could be derived from body reserves. We also assumed that when cows were fed a more energy-dense ration and were still lacking in nutrients, intake would increase an arbitrary 3%. These animal responses are rather optimistic and favor milk production. But depending on the genetics of the animals, physiological status of the cows (parity, stage of lactation, and other considerations), and the type of ration, among other factors, the proportion of energy consumed stored in body reserves could be greater than the 50% assumed herein.

Lastly, the discussion about changes in milking performance (and economic returns) of groups of cows fed rations designed for different levels of production also applies to the literature, wherein groups of cows are fed a treatment diet designed for a given level of milk yield, but that level is seldom specified and could influence the overall results observed for a particular treatment depending on the distribution of milk yield of the cows offered that ration. Thus, it is desirable that future studies would indicate the level of production at which the ration was formulated for each treatment group.

SUMMARY

In summary, EMP is influenced by a wide range of factors, including the physiological status of the cow, digestive function, metabolic partitioning, genetics, and the ration being fed. In terms of biology, EMP will be influenced by rearing practices, as they affect the proportion of nutrients used by the herd that are devoted to growing heifers or to producing milk, and by the reproductive performance of the herd, as this will dictate the proportion of cows in different stages of lactation. Excessive environmental heat or cold, as well as presence of disease or inflammation, also hinder EMP. Digestive function influences EMP because it controls the proportion of nutrients consumed that will be available to the cow. However, relatively large variation occurs between cows in their ability to digest a similar ration, which is partly dictated by their feeding behavior and the microbial population of their digestive tract. Values reported in the literature about the amount of energy realized in milk seem lower than could be expected based on energy consumed. Part of this discrepancy is likely due to an underestimation of energy needs for maintenance, but it is also likely due to decaying marginal efficiencies of conversion of both consumed energy and protein into milk, as level of milk production increases the consequence of reductions in digestibility (due to increased intake) and changes in intermediary and mammary metabolism. Lastly, despite the fact that FE has not been included in genetic schemes, it has increased throughout the years due to progressive improvements in milk yield, although further enhancements due to this mechanism seem unlikely.

In terms of economics, increasing milk production will almost always result in improved profits; however, with high milk yields, caution should be applied when milk price is low or feed cost is high, because marginal improvements in milk yield may be exceeded by marginal increases in variable costs such as feed due to diminishing improvements in nutrient utilization and increasing costs of the feed provided. This is especially the case when feeding groups of cows at high levels of production, because seeking further increases in milk

by providing additional nutrients may not maximize total IOFC, even if FE or yield marginally increase. For this reason, IOFC, not FE or milk yield, is the most relevant parameter to measure and maximize. Income over feed cost is affected by physiological status, digestive function, metabolic partitioning, genetics of cows, and nutritional management of the herd, mainly the target level of production and the distribution of cows among different production (or nutrient requirement) levels.

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